

A NEW LIZARD OF THE GENUS *ARTHROSAURA* (TEIIDAE) FROM SOUTHERN VENEZUELA

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Abstract. — *Arthrosaura synaptolepis*, new species, is a microteiid lizard from highland localities (1200–1450 m) on Cerro de la Neblina and Pico Tamacuari in the borderland between Venezuela and Brazil. It differs from all other *Arthrosaura* in lacking prefrontal scales and in having two (vs. three) pairs of genials. These diagnostic characters seem to have arisen from fusions of a more primitive set of head plates. Other morphological characters and their distributions on the Guayana Highlands suggest that *Arthrosaura synaptolepis* may be the sister species of *A. tyleri*.

Resumen. — El lagarto *Arthrosaura synaptolepis*, especie nueva, es un microtéido de localidades altas (1200–1450 m) en el Cerro de la Neblina y el Pico Tamacuari en la frontera entre Venezuela y Brasil. Se distingue de todas las demás especies de *Arthrosaura* por carecer de escamas prefrontales y en que tiene dos (en vez de tres) pares de geniales. Estos atributos diagnósticos parecen haberse derivado por fusiones de conjuntos más primitivos de escamas de la cabeza. Otras características morfológicas, y distribucionales incluyendo algunos tepuis venezolanos, sugieren que *Arthrosaura synaptolepis* es la especie hermana de *A. tyleri*.

Recent explorations in the broken highlands of extreme southern Venezuela revealed the existence of many undescribed species in the montane herpetofaunas (McDiarmid & Paolillo 1988, Donnelly & Myers pers. obs.). The present description is of a small lizard discovered at disjunct localities on the Brazilian border during expeditions sponsored by the Venezuelan Fundación para el Desarrollo de las Ciencias Físicas, Matemáticas y Naturales (FU-DECI).

Materials and Methods

The three specimens in the type series of the new species are shared among the collections of the American Museum of Natural History, New York (AMNH), the Museo Biología of the Instituto de Zoología Tropical, Universidad Central de Venezuela, Caracas (MBUCV), and the National

Museum of Natural History, Washington, D.C. (USNM). The specimen to be catalogued at MBUCV is parenthetically identified by a USNM catalog number at first citation.

We also examined the following congeneric specimens: *Arthrosaura kockii*. Surinam: Brokopondo: Brownsberg, Mazaroni Plateau, 500 m, AMNH 119400–05. *Arthrosaura reticulata*. Venezuela: Amazonas: Neblina Base Camp on Río Mawarinuma, 140 m (00°50'N, 66°10'W), AMNH 133664–65, USNM 317874–79. *Arthrosaura tyleri*. Venezuela: Amazonas: Cerro Duida, 2164 m, AMNH 36643–45 (type series of *Pantodactylus tyleri*). Bolívar: Meseta de Jaua, 1750–1800 m, USNM 317880. *Arthrosaura versteegii*. Surinam: Brokopondo: 65 km (airline) SSE Paramaribo, 80 m, AMNH 108772, 108774.

Scale lengths were measured to the near-

est 0.1 mm with an ocular micrometer in a dissecting microscope. Measurements to the nearest 0.1 mm were taken with digital calipers of: snout to vent length (SVL), straight line distance from tip of snout to vent; head length (HL), tip of snout to posterior margin of tympanum; maximum head width; maximum head depth; body length (BL), axilla to groin from posterior margin of arm to anterior margin of the leg; forelimb length, from axilla to tip of fourth finger; hind limb length, from groin to tip of fourth toe; and tail length, from vent to tip of tail (regenerated portion separated by + sign).

Arthrosaura synaptolepis, new species
Figs. 1, 2A, 3, 5A, B

Holotype.—USNM 317882 (field no. RWM 18167), an adult male collected by Alfred L. Gardner, 27 Feb 1985, at Camp XI, about 6.2 km NNE Pico da Neblina, 1400–1450 m, Cerro de la Neblina, Amazonas, Venezuela (00°51'45"N, 65°58'52"W).

Paratypes.—MBUCV [formerly USNM 317881 (field no. FGT 3238)], a female collected by Fred G. Thompson, 14 Apr 1984, Camp V, about 2 km NNW Pico da Neblina, 1250 m, Cerro de la Neblina, Amazonas, Venezuela (00°49'10"N, 66°00'02"W). AMNH 134195 (field no. CWM 18768), a female collected by C. W. Myers, 11–17 Mar 1989, at the north base of Pico Tamacuari, 1200–1260 m, in the Sierra Tapirapécó, Amazonas, Venezuela (01°13'N, 64°42'W).

Etymology.—The species name, a noun in apposition, is derived from the Greek *synaptos* (joined together) + *lepis* (scale) in allusion to the apparent fusions that gave rise to a reduced number of head plates in this lizard.

Diagnosis.—A small highland species of *Arthrosaura* that differs from all others in lacking prefrontals and in having two pairs rather than three pairs of genials. See Intra-generic Comparisons for additional differ-

ences between *Arthrosaura synaptolepis* and the four other currently recognized species (*kockii*, *reticulata*, *tyleri*, *versteegii*).

Description of type series.—The series comprises the male holotype (51 mm SVL) and two female paratypes (45–46 mm SVL); see Table 1 for measurements. Head length 19–22% SVL, 1.3–1.6 times longer than wide, 1.3–1.7 times wider than high. Neck as wide as head and anterior body. Body cylindrical, slightly depressed. Complete tail 2.0 times SVL in AMNH 134195, squarish in cross section at base, tapering toward tip. Limbs pentadactyl, all digits with terminal claws. Forelimbs 21–23% SVL, hind limbs 34–35% SVL; adpressed limbs overlapping slightly (1–2 lateral scales). Tongue lanceolate, covered with imbricate scale-like papillae arranged in oblique rows, tip bifid, smooth; 4/4 oblique infralingual plicae. Anterior teeth conical; posterior teeth laterally compressed, bicuspid or tricuspid.

Head relatively short, depressed; snout rounded (Fig. 1). Rostral wider than deep, visible from above, laterally in contact with nasal and first supralabial, dorsally in contact with frontonasal. Frontonasal hexagonal with concave posterior border, separating nasals. Frontal pentagonal, longer than wide. Two pentagonal frontoparietals with a short median suture. Interparietal pentagonal, longer than wide, with a straight posterior margin. Parietals longer than wide, wider than interparietal. Five rectangular occipitals (postparietals), tending to be shorter and wider than dorsal neck scales; lateralmost occipitals smaller than subequal central scales in Neblina specimens, median scale smallest and others subequal in AMNH paratype (Fig. 1). Three supraoculars in direct contact with superciliaries, anterior-most smallest, posteriormost slightly larger or equal to central scale. Nostril in ventral half of undivided nasal. Loreal longer than wide, separated from second supralabial by preocular. Preocular triangular, small, in contact with loreal anteriorly, first subocular posteriorly, and second supralabial

ventrally. Three suboculars; suture between second and third centered beneath pupil. Two or three postoculars (2/2 in holotype, 3/2 in MBUCV paratype, 3/3 in AMNH paratype). Four or five superciliaries (5/5 in holotype and MBUCV paratype, 4/4 in AMNH paratype), anteriormost large, second and third thin and elongate, posteriormost small and round. Temporal region with smooth, pentagonal, juxtaposed scales in four rows; 3–5 temporals between postocular series and scales bordering ear opening (3/4 in holotype, 4/4 in MBUCV paratype, 5/5 in AMNH paratype). Ear opening higher than wide, rounded anterior margin bordered by small scales projecting posteriorly; posterior margin straight; auditory meatus shallow, tympanum visible. Six supralabials, fourth under eye, fifth largest, second smallest; one elongate scale between supralabial series and ear opening. Lower eyelid with a translucent disk of 2–3 large, non-pigmented scales (2/2 in holotype, 3/2 in MBUCV paratype, 3/2 in AMNH paratype); one row of small scales between the superciliary series and the upper eyelid ciliae. Pupil round.

Mental with slightly concave posterior margin. Postmental large, heptagonal, wider than long, in lateral contact with infralabials 1 and 2. Two pairs of genials (large paired scales posterior to the postmental, lying between the infralabials and generally in contact with each other medially); anterior pair longest and in contact with infralabials 2 and 3; posterior pair in contact with infralabials 3 and 4, in medial contact in holotype and MBUCV paratype but separated by one scale in AMNH paratype. A pair of enlarged postgenials or pregulars in posterior contact with second pair of genials; the paired pregulars medially separated by a cluster of 4–8 scales (4 in holotype, 7 in AMNH paratype, 8 in MBUCV paratype) and anterolaterally well separated from last infralabial. Five infralabials.

Head scales smooth, with numerous pores, which tend to be most concentrated

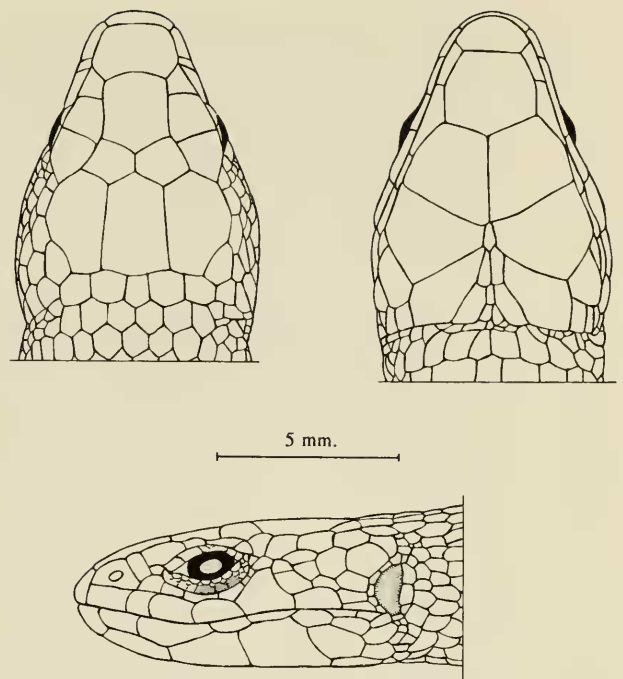


Fig. 1. Head of *Arthrosaura synaptolepis* in dorsal, ventral, and lateral views (AMNH 134195, female paratype). Translucent disk scales of lower eyelid are shaded gray.

around margins of head plates and temporal scales.

Five or six transverse rows of gulars between pregulars and collar scales (6 in holotype and AMNH paratype, 5 in MBUCV paratype); gular scale size increases and the gular number decreases posteriorly; gulars imbricate, with rounded posterior margins. Collar row with five scales, longer than wide, the lateral scales smallest. Two or three rows of small scales hidden by posterior margin of collar; scales largest in posterior row, less than one-third length of ventral scales. Side of neck anterior to arm with medium-sized, rounded, juxtaposed scales; axillary region with smaller, round juxtaposed scales.

Dorsal and lateral body scales of equal size; pentagonal (appearing hexagonal owing to imbrication), weakly keeled, imbricate, mucronate, with pores on posterior margins; scale length more than twice scale width, in 28–30 transverse rows from occipitals to posterior margin of leg (29 in holotype, 28 in MBUCV paratype, 30 in AMNH paratype); transverse rows parallel;

no middorsal discontinuity in scale size. Ventrals smooth, rectangular, imbricate with rounded posterior margins; in eight longitudinal and 18–20 transverse rows (18 in holotype and MBUCV paratype, 20 in AMNH paratype). Scales around midbody 35–36 (35 in holotype, 36 in paratypes).

Six preanal scales, including one large anterior scale and a row of five posterior scales just anterior to vent. Male holotype with 2/2 preanal pores and 5/4 femoral pores, each pore surrounded by three scales; pores absent in females.

Dorsal and lateral caudal scales pentagonal, weakly keeled, mucronate, imbricate, in transverse rows. Subcaudals smooth, imbricate, with rounded posterior margins; larger than dorsal and lateral caudal scales. Eighty-three whorls of caudal scales in the AMNH paratype; ratio of number of whorls to mm of tail length 0.92–1.04 (0.97 in holotype).

Anterodorsal surface of arm with large, smooth, rhomboidal, imbricate scales that are more than twice the width of dorsal body scales. Posteroventral surface of arm with small, round, juxtaposed scales. Anteroventral surfaces of leg with large, smooth, rhomboidal, imbricate scales that are more than twice the width of dorsal body scales. Posterior leg surfaces and ankle with small, round, imbricate scales. Palms and soles with small, round, juxtaposed scales that are not thickened or raised.

Subdigital lamellae as follows (Roman numerals = digits, Arabic numbers = subdigital lamellae on left/right feet); only longest (4th) digits show variation (separate counts given for holotype, MBUCV, and AMNH paratypes, respectively): Forefoot, I 2/2 II 7/7 III 11/10 IV 11/10, 12/13, 11/11 V 7/7. Hind foot, I 3/3 II 8/8 III 11/11 IV 16/16, 18/17, 15/15 V 10/9.

Coloration in life.—Dorsal surfaces brown (Neblina male holotype and Tamacuari female) or grayish black (Neblina female), and dorsal body scales with darker brown to

blackish anterior and posterior margins. A discontinuous yellowish tan dorsolateral line extends posteriorly from above shoulder onto tail base of Neblina male; this pale dorsolateral line (color not noted) distinct only anteriorly and posteriorly in Neblina female, absent in Tamacuari female. Sides of body with several (2–6 per transverse scale row) pale spots on posterior halves of lateral scales (yellowish tan in male, not recorded from living females); these pale spots aligned in Neblina specimens as one (female) or two (male) discontinuous lateral-ventrolateral lines. Pale labial spots white (holotype) or tan (Tamacuari) in life. Tendency for a few light spots (living color not noted) on posterior thigh surfaces.

The ventral surfaces of body, limbs, and tail of the Neblina male were bright red-orange with a paler V-shaped mark outlining lower jaw. Similarly, the ventral surfaces of the Tamacuari female were entirely orange, which was darkest and brightest beneath hind limbs and tail. In contrast, the Neblina female had a light gray throat, pale yellow venter, yellowish gray beneath forelimbs, yellowish brown beneath hind limbs, and bright red beneath proximal third of tail. Iris dark brown.

In preservative, the sides of the body are perceived as being darker in the male than in the females (Fig. 2): the flanks of the male are much darker brown than the dorsum, whereas the flanks of the females are about the same (Neblina) or only slightly darker (Tamacuari) than the dorsum. The ventral surfaces turned pale tan in preservative; dark brown flecking is on the lateral margins of the chin shields and gulars; palms and soles are brown; tail tip of Tamacuari specimen is dark brown.

Hemipenis.—The genitalia of the holotype were everted in the field and the left organ was subsequently removed for study and illustration (Fig. 3). The hemipenis is bilobed; the lobes are short and irregularly flattened terminally. The shallow sulcus

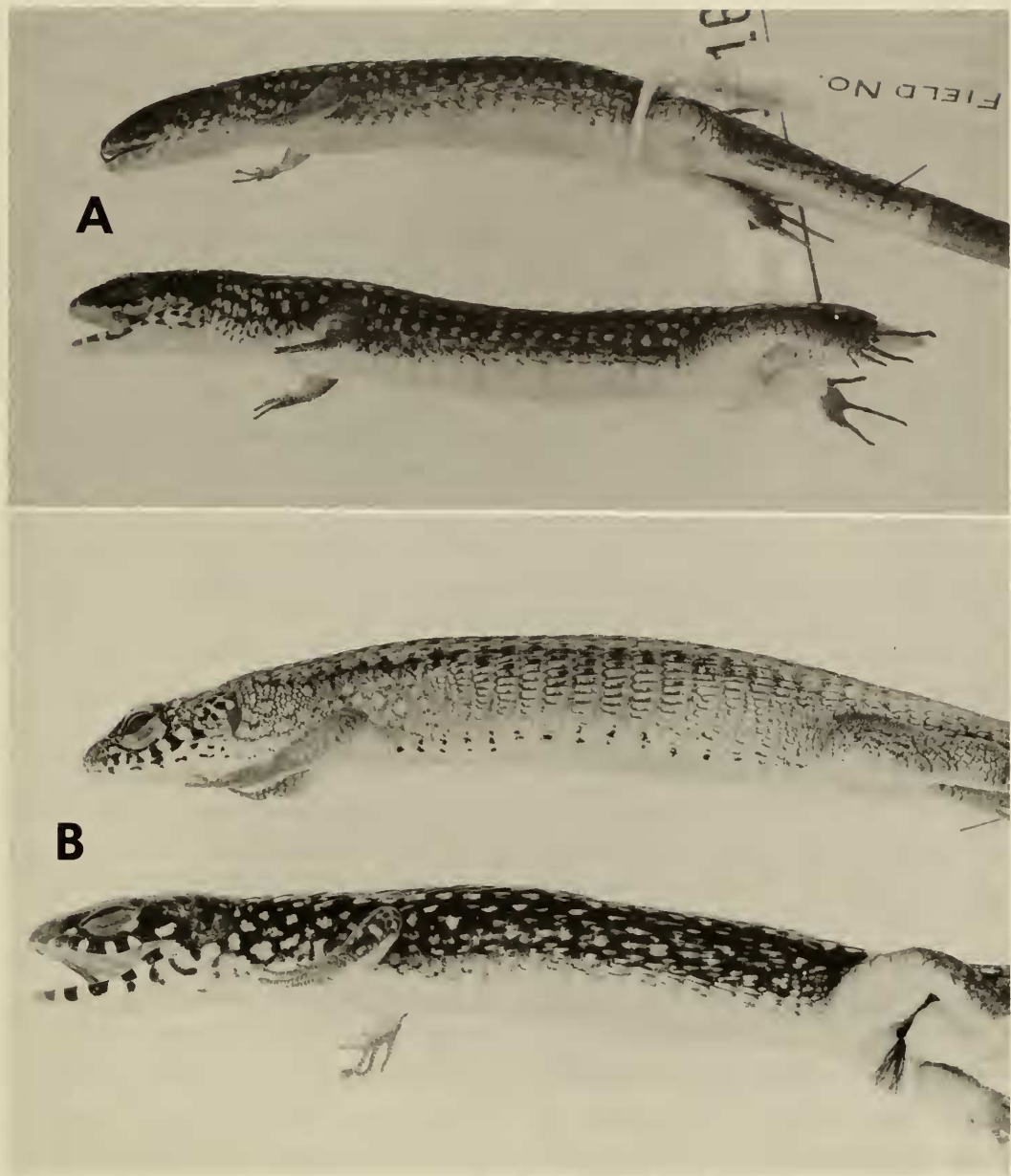


Fig. 2. Lateral views showing sexual dichromatism in (A) *Arthrosaura synaptolepis* (MBUCV female paratype and male holotype) and (B) *A. reticulata* (USNM 317877, female, and AMNH 133665, male), from 1250–1450 m and 140 m (respectively) at Cerro de la Neblina, all $\times 1$. Males (lower specimen of each pair) tend to have darker sides than females, which is most pronounced in *A. reticulata*.

spermaticus runs a medial course to bifurcate at a pronounced elevation of tissue in the crotch of the organ; the sulcus branches extend centripetally towards the apices of the lobes, but the branches are broad, shallow, and poorly defined. Transversely aligned plicae arise on either side of the midline of the asulcate surface and extend around to the sulcate surface, terminating well short of the sulcus spermaticus. The

plicae comprise myriad microscopic, calcified spinules, but some spinules on the sides of the organ are larger than others (Fig. 3).

Distribution and habitat.—*Arthrosaura synaptolepis* is known from only two highland (1200–1450 m) localities, Cerro de la Neblina and Cerro Tamacuari, in the borderland between Venezuela and Brazil. Cerro de la Neblina is an immense tepui (table

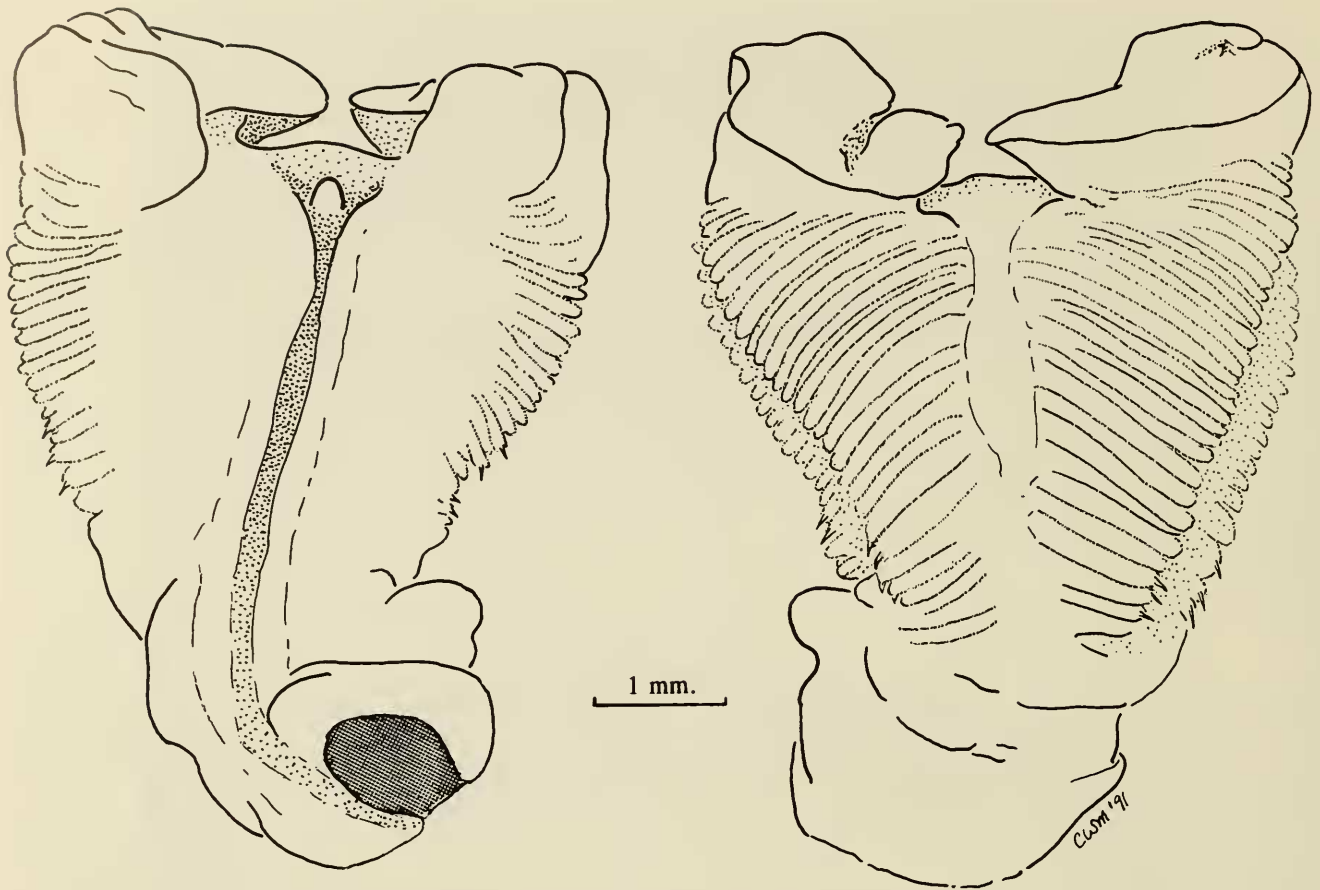


Fig. 3. Everted hemipenis of *Arthrosaura synaptolepis*. Left organ of the holotype.

mountain) that is nearly split by a great canyon. Cerro Tamacuari is not a tepui, although probably a remnant of the same ancient highland. The prominent peaks on these two mountains are on the international border; Pico Tamacuari is about 150 km ENE of Pico da Neblina.

The male holotype was collected about 1500 h along a trail through a dense patch of pitcher plants of the genus *Heliamphora*. The other Neblina specimen was crawling in leaf litter on the forest floor in camp at 1000 h. The Tamacuari specimen was collected on the forest floor by day, on a slope above a rocky stream.

Intragenetic Comparisons

Cunha (1967), whose arrangement was followed by Peters & Donoso-Barros (1970), recognized four species in the genus *Arthro-*

saura: *A. amapaensis* Cunha,¹ *A. kockii* (Van Lidth de Jeude), *A. reticulata* (O'Shaughnessy), and *A. versteegii* Van Lidth de Jeude. Following Brongersma (1935), Hoogmoed (1973) treated *A. versteegii* as a subspecies of *A. reticulata* and placed *A. amapaensis* in the synonymy of *A. reticulata versteegii*. Recently, however, Hoogmoed & Avila Pires (pers. comm.) decided to remove *A. versteegii* and *A. [=Pantodactylus] tyleri* (placed in synonymy by Cunha [1967]) from the synonymy of *A. reticulata*. Based on the American Museum types, we had independently reached the same conclusion on the validity of *A. tyleri*, and we also concur with Hoogmoed & Avila Pires' proposed resur-

¹ Authors have followed Cunha's incorrect use of the neuter ending (*amapaense*) for this species name (described in *Arthrosaura*, feminine).

rection of *A. versteegii*. In their yet unpublished manuscript, Hoogmoed & Avila Pires (pers. comm.) provide a historical review and detailed accounts for the species of *Arthrosaura* with three supraoculars (*A. reticulata*, *A. tyleri*, and *A. versteegii*).

Following, we compare the new species (first value in parentheses) with the four other species of *Arthrosaura* now recognized (second value in parentheses).

Arthrosaura synaptolepis differs from *A. kockii* in the number of supraoculars (3 vs. 4), size, morphology, and number of temporal scales (large and smooth in 4 rows vs. small and keeled in 8 rows), size and shape of lateral neck scales (moderate and round vs. small and granular), degree of keeling of dorsal scales (weakly vs. strongly keeled), presence or absence of keels on dorsal limb scales (smooth vs. keeled), color pattern (no middorsal light stripe vs. middorsal light stripe present), and amount of overlap between adpressed limbs (slight, 1–2 lateral scales vs. substantial, 6+ scales). *Arthrosaura kockii* usually has a proportionately longer head than *A. synaptolepis* (based on data presented for *A. kockii* by Hoogmoed 1973: table 14 [excluding data for RMNH 15226, for which HL seems too small for the given SVL]): Ratio of head length to SVL in *A. synaptolepis* is 0.19–0.22 (0.206 ± 0.015 , $n = 3$); HL/SVL in *A. kockii* is 0.20–0.30 (0.266 ± 0.019 , $n = 42$). See Table 2 for differences in ratios and selected scale counts among *A. synaptolepis* and the remaining three species of *Arthrosaura* (*reticulata*, *tyleri*, and *versteegii*)—all characterized by three supraoculars.

Arthrosaura synaptolepis differs from *A. versteegii* in having fewer and larger temporals (4 rows vs. 6–7 rows), size of lateral neck scales (moderate vs. small), size of scales in axilla and groin (small vs. granular), and morphology of the subcaudal scales (pentagonal and imbricate vs. rectangular and juxtaposed).

Arthrosaura synaptolepis was compared

Table 1.—Measurements for the type series of *Arthrosaura synaptolepis*.

| Character | Holotype male | MBUCV paratype female | AMNH paratype female |
|-------------------|---------------|-----------------------|----------------------|
| Snout–vent length | 51.0 | 45.4 | 46.1 |
| Tail length | 9.2 + 4.2 | 19.3 + 38.7 | 90.5 |
| Head length | 10.8 | 9.9 | 8.7 |
| Head width | 6.6 | 6.0 | 6.7 |
| Head depth | 5.2 | 4.0 | 4.0 |
| Body length | 26.3 | 22.5 | 23.7 |
| Forelimb length | 11.6 | 10.0 | 9.5 |
| Hind limb length | 17.7 | 15.3 | 15.8 |

with several specimens of *A. reticulata* collected at the base of Cerro de la Neblina, a sample that agrees with the account of *reticulata* being prepared by Hoogmoed & Avila Pires (pers. comm.). *Arthrosaura synaptolepis* differs from these specimens in the number and size of temporal scales (4 rows of large scales vs. 6–7 rows of small scales), size of lateral neck scales (moderate vs. small), size of scales in axilla and groin (small vs. granular), degree of keeling of dorsal body scales (weakly vs. moderately keeled), amount of overlap between adpressed limbs (slight, 1–2 lateral body scales vs. moderate to substantial, 3–6 scales), and details of pigmentation (dorsal body scales with dark margins vs. dorsal scales irregularly flecked with black). The apparent common tendency of males to have darker flanks and more distinct pale lateral spots on flanks and tails than females is more strongly pronounced in *reticulata* than in *synaptolepis* (Fig. 2).

Arthrosaura synaptolepis differs from *A. tyleri*, the other tepui species, in degree of keeling of dorsal body scales (weakly vs. strongly keeled), shape of median subcaudal scales (pointed vs. rounded posterior margins), ventral pigmentation (immaculate ventrals vs. heavily pigmented ventrals, see Fig. 4), and amount of overlap of adpressed limbs (slight, 1–2 lateral body scales vs. moderate, 3–4 scales).

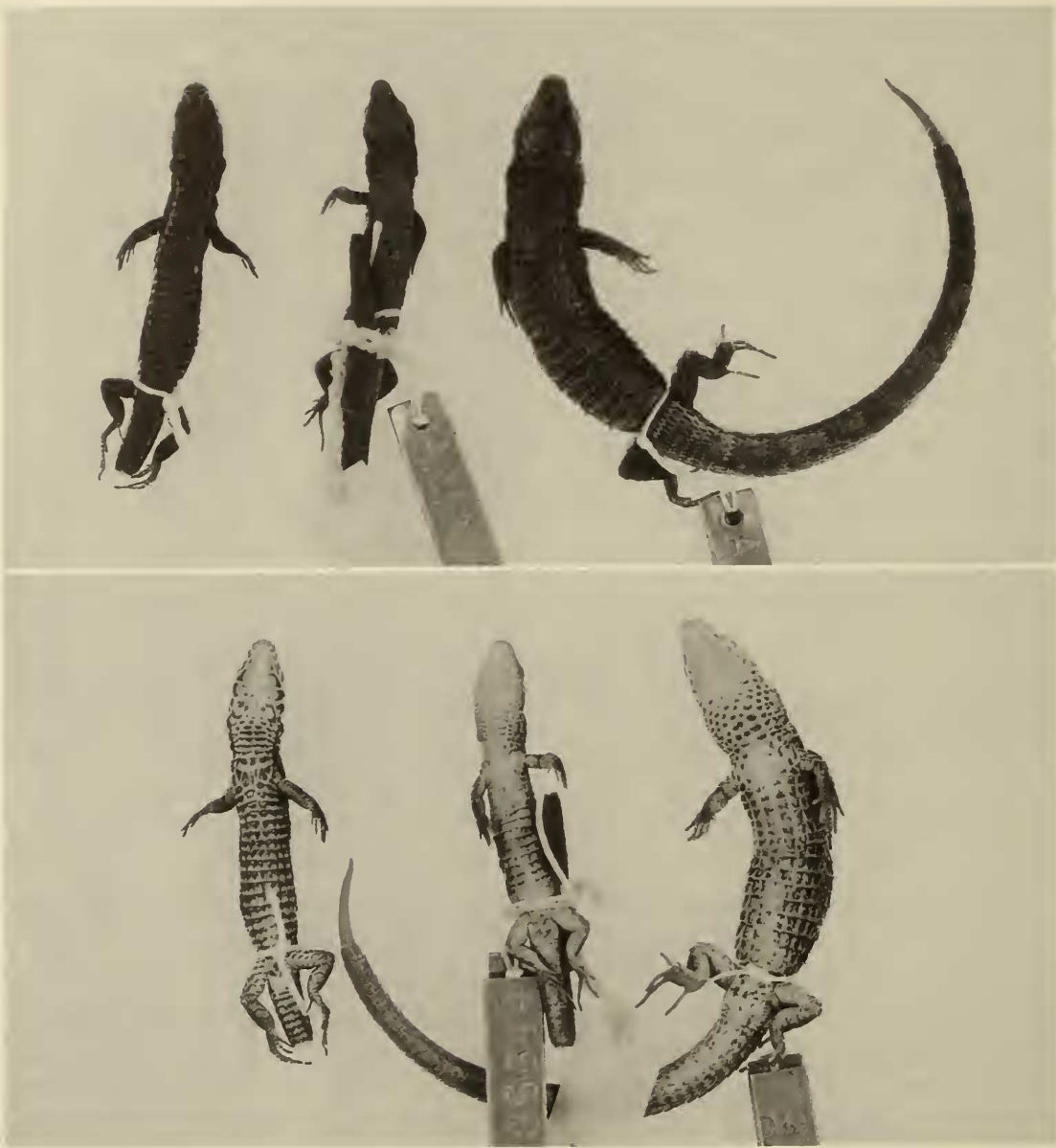


Fig. 4. Dorsal and ventral views of *Arthrosaura tyleri*, $\times 1$. Left to right: USNM 317880, AMNH 36644 (paratype), AMNH 36645 (holotype).

Heretofore, *Arthrosaura tyleri* (Fig. 4) was only known from the type series of three females from over 2000 m elevation on the summit of Cerro Duida. An additional specimen referable to *A. tyleri* is from 1750–1800 m on Meseta de Jaua, roughly 200 km NE of Duida. Although the Jaua specimen has a more rounded snout than the Duida types and an extra genial on the left side, we were unable to otherwise distinguish it morphologically. The Jaua lizard, a male, is darker than the females from Duida and has a series of light dorsolateral spots, but these differences are suggestive of the sexual

dichromatism in *A. synaptolepis* and *A. reticulata*.

Ruibal (1952:512), in removing *tyleri* from *Pantodactylus*, suggested that *Arthrosaura tyleri* was related to *A. kockii*, but gave no reasons that exclude a close relationship with one of the species with three supraocular scales. In any case, under the assumption that some unknown portion of the morphological resemblance reflects synapomorphy, *Arthrosaura synaptolepis* may be the closest relative (sister species) of *A. tyleri*. These “tepui species” have fewer mid-body scale rows, temporal rows, and sub-

Table 2.—Scale counts and ratios for *Arthrosaura* species with three supraoculars. Values are means \pm one standard deviation, range in parentheses.

| Character | <i>A. synaptolepis</i> (n = 3) | <i>A. tyleri</i> (n = 4) | <i>A. reticulata</i> (n = 8) | <i>A. versteegii</i> (n = 2) |
|-------------------------------|-----------------------------------|---------------------------------|---------------------------------|---------------------------------|
| Transverse ventrals | 18.7 \pm 1.15 (18–20) | 17.8 \pm 0.96 (17–19) | 17.0 \pm 0.47 (17–20) | 16.5 \pm 0.71 (16–17) |
| Transverse dorsals | 29.0 \pm 1.00 (28–30) | 28.5 \pm 0.58 (28–29) | 28.1 \pm 0.99 (27–30) | 26.0 \pm 0.00 (26) |
| Scales around midbody | 35.7 \pm 0.58 (35–36) | 34.5 \pm 4.12 (31–39) | 41.5 \pm 1.85 (40–45) | 41.0 \pm 0.00 (41) |
| Temporal rows | 4.0 \pm 0.00 (4) | 3.8 \pm 1.04 (3–4) | 7.3 \pm 2.41 (6–7) | 6.5 \pm 0.58 (6–7) |
| Palpebrals | 2.7 \pm 0.82 (2–4) | 2.3 \pm 0.46 (2–3) | 3.6 \pm 0.81 (2–5) | 2.5 \pm 0.58 (2–3) |
| Subdigital lamellae finger IV | 11.3 \pm 1.03 (10–13) | 11.8 \pm 1.17 (10–13) | 16.1 \pm 1.44 (13–18) | 13.0 \pm 0.82 (12–14) |
| Subdigital lamellae toe IV | 16.2 \pm 1.17 (15–18) | 18.8 \pm 1.67 (16–21) | 20.8 \pm 1.57 (17–22) | 18.5 \pm 0.58 (18–19) |
| Head length/SVL | 0.21 \pm 0.004 (0.21–0.22) | 0.24 \pm 0.013 (0.23–0.25) | 0.23 \pm 0.014 (0.22–0.26) | 0.27 \pm 0.019 (0.26–0.29) |
| Postmental length/HL | 0.24 \pm 0.024 (0.22–0.27) | 0.16 \pm 0.029 (0.12–0.19) | 0.17 \pm 0.008 (0.16–0.18) | 0.16 \pm 0.005 (0.16–0.17) |
| Forelimb length/BL | 0.43 \pm 0.027 (0.40–0.44) | 0.51 \pm 0.052 (0.46–0.58) | 0.57 \pm 0.051 (0.47–0.63) | 0.55 \pm 0.173 (0.42–0.67) |
| Hind limb length/BL | 0.67 \pm 0.010 (0.66–0.68) | 0.80 \pm 0.040 (0.75–0.84) | 0.95 \pm 0.101 (0.81–1.10) | 0.78 \pm 0.171 (0.66–0.90) |

digital lamellae (Table 2) than lowland *Arthrosaura*. The low number of midbody scale rows is a manifestation of the relatively large dorsal and ventral scales of *Arthrosaura synaptolepis* and *A. tyleri*. Similarly, these are the only species with large smooth scales in the temporal region, accounting for the low number of temporal rows. The tepui species, *Arthrosaura reticulata*, and *A. versteegii* have three supraoculars and differ from *A. kockii* which has four.

The highland localities of the presumed sister species, *Arthrosaura synaptolepis* and *A. tyleri*, are well separated. The two tepuis from which *tyleri* is known are roughly 200 km apart and the two localities for *synaptolepis* are about 150 km from one another. The closest localities (Duida and Tamacuari) between the northern *tyleri* and the southern *synaptolepis* are 250 km apart. Intraspecific variation in the genials of *A. tyleri* helps explain the origin of one of the two autapomorphies of *A. synaptolepis*.

Origin of Diagnostic Characters

Arthrosaura synaptolepis has a relatively shorter head than other species of *Arthrosaura* (Table 2 and Intrageneric Comparisons). This condition is reflected in two characters of *A. synaptolepis* that are unique in the genus: (1) the absence of prefrontal scales and (2) the presence of two rather than three pairs of genials (or, depending on definitions, three rather than four pairs, see below). These seem to be derived features from the fusion of certain head scales. We use the word “fusion” in the sense of phylogenetic transformation and imply nothing about ontogenetic transformation for which no data exist.

Species of *Arthrosaura* typically have a pair of prefrontal scales bounded anteriorly by a large frontonasal, posteriorly by a hexagonal frontal, and laterally by the loreal and the first, or first and second, supraocular scales. In *A. synaptolepis*, the prefrontals are

absent; the frontonasal is large and has a medially indented or concave frontal suture in contrast to a medially pointed frontal suture in other species (compare Figs. 1 and 5A [*synaptolepis*] with 5C [*tyleri*] and with figs. 43 [*kockii*] and 45 [*versteegii*] in Hoogmoed, 1973). One of the paratypes has a short (about 0.2 mm) suture extending mediad from each loreal (Fig. 5A); these symmetrical but incomplete sutures appear to be vestiges of the original frontonasal-prefrontals suture (compare Fig. 5C).

Arthrosaura spp. typically have a single postmental followed by three pairs of genials; the usual arrangement of ventral head shields in these lizards is as follows: a postmental is in contact with infralabials 1 and 2 laterally and with the first pair of genials posteriorly; the first pair of genials are in medial contact and in contact with infralabials 2 and 3 laterally; the second pair of genials are in medial contact and in contact with infralabials 3 and 4 laterally; the third pair of genials are separated by 1–3 scales and in contact with infralabials 4 and 5 laterally. A pair of large pregenials or postgenials are in contact anteriorly with the posterior margins of the last pair of genials;² the pregenials are separated medially by a cluster of 5–11 small juxtaposed scales that vary in size, shape, and number; the pregenials are well separated from the infralabials. Minor exceptions to this arrangement include an example of *A. reticulata* from the base of Cerro de la Neblina (USNM 317875), whose postmental is in contact with infralabials 1–3 (vs. 1–2) on the right side.

² We somewhat arbitrarily define genials as large paired plates that are usually in contact with the infralabials laterally (last pair sometimes narrowly separated from labials) and usually in median contact with one another (except last pair often narrowly, or, in some taxa, widely separated). The “pregenials” often are considered as being the fourth (i.e., the posterior-most) pair of genials or “chin shields” in the microteiid literature, but, when present, they vary greatly in size and shape.

Arthrosaura synaptolepis is the only species in the genus having two rather than three pairs of genials as defined herein. The postmental is much longer in *A. synaptolepis* than in the other species of *Arthrosaura* with three pairs of supraoculars (Table 2); therefore, on topographic grounds we hypothesize that this enlargement seemingly represents the fusion of the postmental with a primitive first pair of genials. Thus, the first pair of genials in *A. synaptolepis* represent the elongate second pair of other species; genial pairs one and two in *A. synaptolepis* are equivalent to pairs two and three of other *Arthrosaura*.

This conclusion is supported by a paratype of *A. tyleri* that has aberrant genials (Fig. 5D). This specimen shows three genials (normal in *Arthrosaura*) only on its right side; on the other side it has only two genials, the condition in all *A. synaptolepis*. A short suture extending mediad into the postmental from the left side, level with the anterior part of the second infralabial, suggests a fusion between the postmental and an anterior genial (Fig. 5D). The USNM specimen assigned to *A. tyleri* from Meseta de Jaua varies from the typical arrangement in another direction: it has four genials on the left side of the head, a condition that does not characterize any known species of *Arthrosaura*.

Some Intergeneric Comparisons

Our suggestion that a lack of prefrontals and a reduced number of genials are derived character states in *Arthrosaura synaptolepis* is based, in part, on ingroup (intrageneric) variation, inasmuch as we are uncertain about the most appropriate outgroups. However, most microteiids have paired prefrontals. Also, three pairs of genials occur in nearly all other genera of microteiids that inhabit the Guiana Shield and this condition seems to be the normal (i.e., presumed primitive) state in most of them (*Alopoglossus*, *Amapasaurus*, *Anadia*, *Ar-*

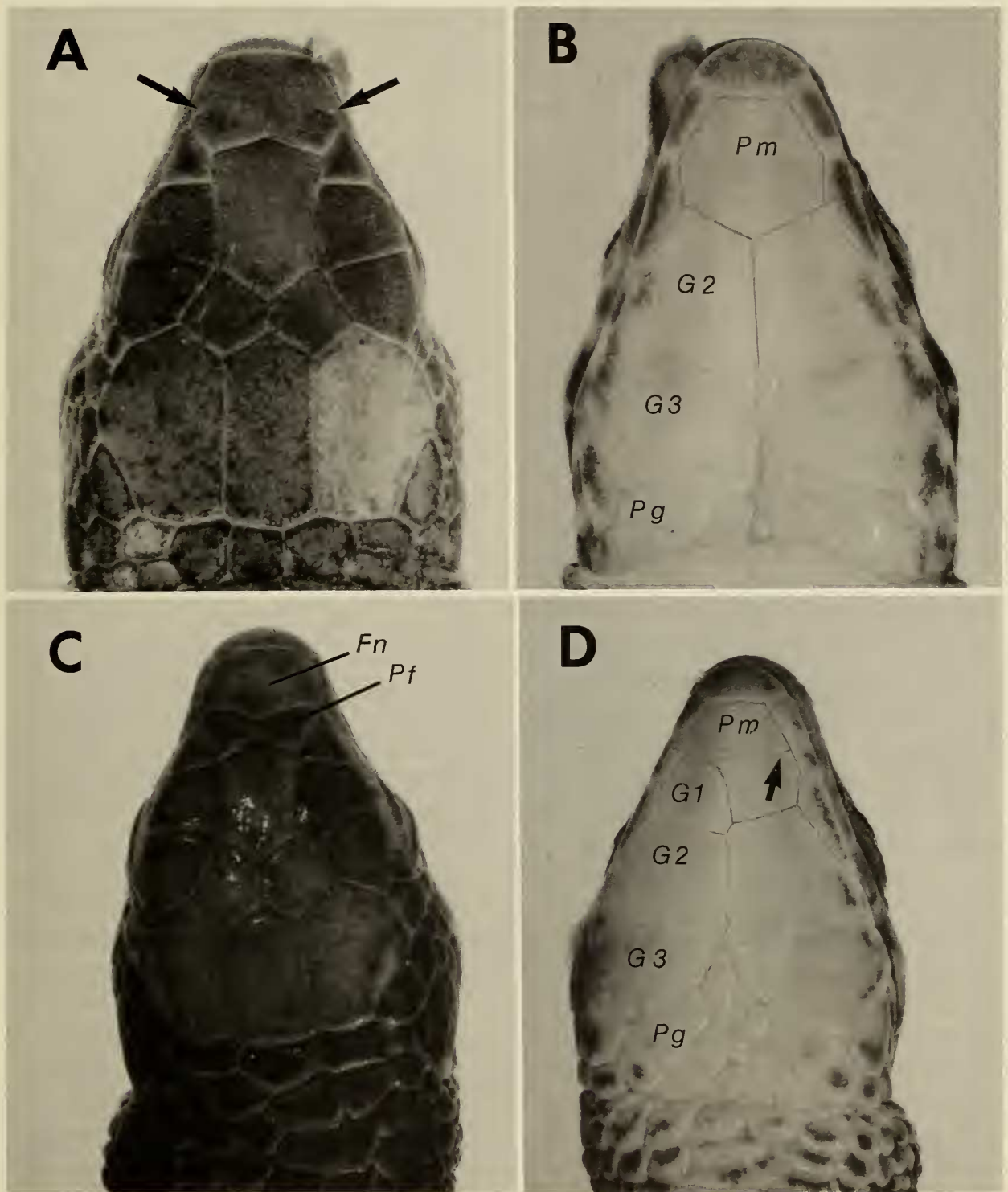


Fig. 5. Dorsal and ventral views of heads of *Arthrosaura synaptolepis* (A–B, MBUCV paratype) and *Arthrosaura tyleri* (C–D, AMNH 36644, paratype), approximately $\times 8$. Abbreviations: Fn, frontonasal; Pf, prefrontal; Pm, postmental; G1–G3, genials 1–3; Pg, large paired pregenial. A. An aberrancy in *A. synaptolepis*: Arrows indicate traces of sutures that separate paired prefrontals from the anterior frontonasal in most species of *Arthrosaura* (as in C below). D. An aberrancy in *A. tyleri*: Arrow indicates trace of suture between postmental and first genial on lizard's left side. Failure of G1 to differentiate from the postmental on the left side produces (asymmetrically) the diagnostic condition of *A. synaptolepis* (as in B above).

throsaura, *Cercosaura*, *Euspondylus*, *Leposoma*, *Prionodactylus*, *Ptychoglossus*, *Riolama*, *Tretioscincus*). The fossorial *Bachia* and the large-scaled *Gymnophthalmus* and *Iphisia* have the size of the ventral head plates much enlarged and the number of plates greatly reduced (with only two pairs of genials in some species of *Gymnophthalmus*); the aquatic or semiaquatic species of *Neusticurus* seem to have either three or four pairs of genials, with the posteriormost pairs widely separated, in correlation with a posterior widening of the head. Presch (1980) placed *Arthrosaura* with several of the above genera (his group 4 = *Arthrosaura*, *Cercosaura*, *Neusticurus*, *Leposoma*, and *Echinosaura*); Presch used osteological data and therefore had to exclude several rare genera, including, for example, *Stenolepis* of northeastern Brazil.

Comparison between *Arthrosaura* and taxa of the Brazilian Shield may eventually prove fruitful in the search for relationships. Boulenger ("1887" [1888]) in fact suggested a relationship between *Arthrosaura* and Brazilian *Heterodactylus* and *Stenolepis*. Both agree with *Arthrosaura synaptolepis* in lacking prefrontals and having only two pairs of genials. They differ from *Arthrosaura* in lacking a collar fold and in having a larger palpebral disk and other details. *Heterodactylus* (in Presch's group 6) furthermore lacks an external ear opening and has very short limbs, with a reduced or absent pollex; distributions of the two species of *Heterodactylus* cluster in southeastern Brazil (see Vanzolini & Ramos 1977).

The monotypic *Stenolepis* from northeastern Brazil (Pernambuco) shows the closest overall resemblance with *Arthrosaura* (based on comparison with one specimen of *Stenolepis ridleyi*, AMNH 131867). If the head-shield resemblances between *Arthrosaura synaptolepis* and *Stenolepis* were homologous, paraphyly of *Arthrosaura* would be suspected. The geographic relationships would not be without precedence, inasmuch as other tepui reptiles may be related to spe-

cies occurring well south of the Amazon (Donnelly & Myers 1991:46, 49; Frost 1992:36). However, the postmental is relatively smaller in *Stenolepis* than in *Arthrosaura synaptolepis* and the first of the two pairs of genials is relatively larger, suggesting that the original first pair of genials apparently fused with the second pair (rather than with the postmental as in *A. synaptolepis*). The subtleties of such variation deserve considerably more attention than usually accorded.

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